Pneumaticity of the dorsal foramen and dorsal sulcus of the sternum in Australasian Passeriformes

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The Passeriformes comprise almost 60% of the 9,000-10,000 recent species of birds (Bock & Farrand 1980, Sibley & Monroe 1990). Songbirds are more widely distributed than any other avian order but aspects of their intra-ordinal classification remain unsettled. Avian systematics have been revitalized in recent years with the increased use of molecular and biochemical techniques (e.g. Christidis & Schodde 1991, Sibley & Ahlquist 1985, 1990). In particular, the classification of the Passeriformes has undergone substantial reorganization (e.g. Sibley & Ahlquist 1985, 1990, Helm-Bychowski & Cracraft 1993; Barker *et al.* 2002; Ericson *et al.* 2002). Members of the Passeriformes share a strikingly similar osteological morphology and the identification of subordinal taxa is purportedly extremely difficult, if not impossible, because of this similarity (Olson 1985). Few characters of the post-cranial skeleton have been studied in any depth; the best known is the pneumotricipital fossa of the humerus (Bock 1962). Here, an osteological character of the sternum is surveyed and the distribution of its character states examined in light of proposed relationships within the Australasian Passeriformes.

Methods

This study focuses on the dorsal pneumatic foramen and dorsal sulcus of the sternum (termed by Baumel & Witmer (1993) as foramen pneumaticum and sulcus medianus sterni, respectively). The sulcus runs anteroposteriorly (craniocaudally) along the midline of the dorsal (visceral) surface of the sternum. The pneumatic foramen lies at the anterior (cranial) end of the sulcus. It may be absent (Fig. 1a). When present, there may be considerable variation in its appearance, from a single and distinct foramen (Fig. 1b) to a group of foramina varying in size (Fig. 1c-e). Smaller foramina may occur around the dorsal foramen area or extend posteriorly from the main dorsal foramen area along the dorsal sulcus, approaching the posterior margin of the sternum (Fig. 1d-e). These are all scored as 'present'.

For the purposes of the following discussion, taxonomic divisions of the Passeriformes above the family level, and their sequence, follow Sibley & Monroe (1990). The sequence and delimitation of Australian families are after Christidis & Boles (1994), as are the names of genera and species. For New Guinea and New Zealand taxa, names follow Beehler & Finch (1985) and OSNZ (1990), respectively.

Sterna were examined from the avian skeleton collections of the Australian Museum, Sydney; Australian National Wildlife Collection, CSIRO Division of

Sustainable Ecosystems, Canberra; Museum Victoria, Melbourne; South Australian Museum, Adelaide; Queensland Museum, Brisbane; Queen Victoria Museum, Launceston; and Museum of New Zealand Te Papa Tongarewa, Wellington. For most species, 1-3 specimens were examined. Greater numbers of Australasian robins (Petroicidae) were available because they had been borrowed for another project. In total, 795 specimens of 268 species of Passeriformes were examined. Representatives of the Piciformes and Coraciiformes were also examined as possible outgroups to determine which character state might be ancestral.

Results

The taxa, number of specimens examined and observed character states are given in Table 1. In representatives of three families of the Piciformes, there was a particular form of the present character state with no distinct pneumatic dorsal foramen; however, small foramina occurred along the caudal half of the dorsal sulcus. This was scored as present. In five families of the Coraciiformes, the pneumatic dorsal foramen and foramina were present in all but a single cerylid kingfisher and one of four alcedinid kingfishers.

Only three families of suboscines (Suborder Tyranni) were examined, the Australian Pittidae, New Zealand Acanthisittidae and non-Australasian Tyrannidae, representing the three infraorders recognised by Sibley & Monroe (1990). Other than one individual of *Pitta*, all specimens of Pittidae and Tyrannidae were scored as 'present'; foramina were absent in three specimens of Acanthisittidae.

In the Suborder Passeri (oscines), in most superfamilies one or both character states can be found, although these show pronounced segregation between families.

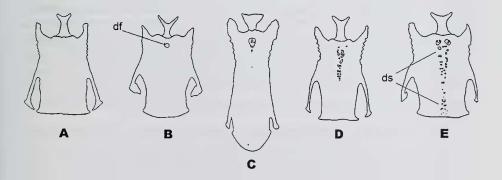


Figure 1: Character states of the dorsal pneumatic foramen and dorsal sulcus of the sternum of Passeriformes. A. Dorsal foramen and accompanying foramina absent (Passeridae: *Passer domesticus*). B-E. Dorsal foramen present, showing extreme and intermediate states of accompanying foramina surrounding the foramen and extending caudally along the dorsal sulcus: B. Pittidae: *Pitta versicolor*; C. Menuridae: *Menura novaehollandiae*; D. Meliphagidae: *Phylidonyris nigra*; E. Pachycephalidae: *Pachycephala simplex*. df = dorsal foramen, ds = dorsal sulcus.

Within the Parvorder Corvida, the Superfamily Menuroidea has the present state in all specimens of the lyrebirds (Menuridae) and bowerbirds (Ptilonorhynchidae), but the absent state in all treecreepers (Climacteridae). A similar disparity is found in the Meliphagoidea. The fairy-wrens (Maluridae) and pardalotes and acanthizid warblers (Pardalotidae) invariably lack any dorsal foramina whereas, other than a few individuals, all honeyeaters and chats (Meliphagidae) have the present character state.

The greatest amount of variation within any Superfamily occurred in the Corvoidea. The presence of a pneumatic dorsal foramen and in some cases a pneumatic dorsal sulcus is most consistently seen in this Superfamily (there were odd individuals lacking this state). This pneumaticity is absent in the logrunners (Orthonychidae), Australo-Papuan babblers (Pomatostomidae) and sittellas (Neosittidae). There were differences between genera in the whipbirds and quail-thrushes (Eupetidae = Cinclosomatidae), whistlers and shrike-thrushes (Pachycephalidae), mudnest builders (Corcoracidae) and New Zealand wattlebirds (Callaeatidae). There was considerable variation both within and between species of the Australasian robins (Petroicidae) and cuckoo-shrikes (Campephagidae).

Variation was minor within the Parvorder Passerida. In the three superfamilies Muscicapoidea, Sylvioidea and Fringilloidea, a sternal foramen was absent, with few exceptions, most of which (6 of 10) were restricted to just three families (Alaudidae, Pycnonotidae, Passeridae).

Discussion

Both the Coraciiformes and Piciformes have sterna with pneumatic foramina. While the Coraciiformes exhibit the general corvoid condition, the condition of this character in the Piciformes differs from that of any of the Passeriformes by lacking a distinct anterior dorsal foramen or foramina. Recent molecular studies have cast doubts on the traditional association of these orders with the Passeriformes (e.g. Sibley & Ahlquist 1990, Mindell *et al.* 1997). It is not currently possible to assess the polarity of the character states. Because it is not known which state is derived, this character cannot be used for decisions about relationships at this time. Nonetheless, some comments can be made about the distribution of these states in light of findings of other authors.

The position of the Acanthisittidae relative to the remainder of the Passeriformes is not settled. Although placed within the Tyranni by Sibley & Monroe (1990), the marked segregation of character states between this family and the other infraorders of suboscines is consistent with the more trenchant differences found by Ericson *et al.* (2002), who placed this family as the sister-group to all other Passeriformes.

As with the pneumotricipital fossa, members of suborders, parvorders, superfamilies and families are generally characterized by a particular state, but there are exceptions. The presence of the sternal pneumatic fossa is the largely predominant state in two infraorders of the suboscines and the subfamilies Corvinae and Dicrurinae

TABLE 1

Distribution of character states (absent or present) of dorsal pneumatic foramina in Australasian Passeriformes together with selected Piciformes and Coraciiformes. Sequence and nomenclature of families generally follows Christidis & Boles (1994), with higher taxonomic divisions following Sibley & Monroe (1990); genera and species are arranged alphabetically within families or subfamilies. The figures following each species' name indicate the number of specimens that exhibited each character state for each taxon (absent/present).

Order Piciformes (0/13)

Picidae (0/11): Colaptes auratus (0/8); Dendrocopos major (0/1); Melanerpes
erythrocephalus (0/1); Picus viridis (0/1)
Lybiidae (0/1): Tricholaema diademata (0/1)
Ramphastidae (0/1): Ramphastos toco (0/1)
Order Coraciiformes (2/33)
Coraciidae (0/4): Euystomus orientalis (0/4)
Alcedinidae (1/6): Alcedo atthis (0/2); A. azurea (1/4)
Halcyonidae (0/21): Dacelo leachii (0/1); D. novaeguineae (0/7); Tanysiptera sylvia (0/1); Todirhamphus macleayii (0/4); T. sanctus (0/6); Syma torotoro (0/1); S. megarhyncha (0/1)
Cerylidae (1/0): Megaceryle alcyon (1/0)
Meropidae (0/2): Merops ornatus (0/2)
Order Passeriformes (336/474)
Suborder Tyranni (4/11)
Infraorder Acanthisittides (3/0)
Acanthisittidae (0/3): Acanthisitta chloris (1/0); X. gilvivenris (1/0); Xenicus longipes (1/0)
Infraorder Eurylaimides (1/7)
Pittidae (1/7): <i>Pitta erythrogaster</i> (1/0); <i>P. versicolor</i> (0/7)
Infraorder Tyrannides (0/4)
Tyrannidae (0/4): Contopus sordidulus (0/1); Empidonax difficilis (0/1); Tyrannus tyrannus
(0/1), T. verticalis (0/1)
Suborder Passeres (332/463)
Parvorder Corvida (219/453)
Superfamily Menuroidea (13/5)
Menuridae (0/5): Menura alberti (0/1); M. novaehollandiae (0/4)
Climacteridae (13/0): Climacteris erythrops (1/0); C. melanura (1/0); C. picumnus (6/0);
Cormobates leucophaeus (4/0); C. placens (1/0)
Superfamily Meliphagoidea (102/126)
Maluridae (21/0): Amytornis dorotheae (3/0); A. woodwardi (2/0); Malurus cyaneus (7/0);
M. cyanocephala (1/0); M. lamberti (6/0); Stipiturus malachurus (2/0)
Pardalotidae: Pardalotinae (7/0): Pardalotus punctatus (1/0); P. striatus (6/0);
Pardalotidae: Dasyornithinae (3/0): Dasyornis brachypterus (3/0)
Pardalotidae: Acanthizinae (66/0): Acanthiza apicalis (2/0); A. chrysorrhoa (2/0); A.
lineata (6/0); A. nana (2/0); A. pusilla (6/0); A. reguloides (1/0); A. uropygialis (5/0);
Aphelocephala leucopsis (2/0); Chthonicola sagittata (5/0); Crateroscelis robusta (1/0);
Gerygone chloronotus (1/0); G. fusca (4/0); G. levigaster (1/0); G. magnirostris (1/0); G.
mouki (2/0); G. olivacea (2/0); G. palpebrosa (1/0); Hylacola cauta (1/0); H. pyrrhopygia
(2/0); Origma solitaria (2/0); Pycnoptilus floccosus (1/0); Pyrrholaemus brunneus (1/0); Sericornis citreogularis (3/0); S. frontalis (5/0); S. magnirostris (6/0); Smicrornis
brevirostris (1/0)

Meliphagidae: Meliphaginae (5/122): Acanthagenys rufogularis (0/4); Acanthorhynchus tenuirostris (1/4); Anthochaera carunculata (0/4); A. chrysoptera (0/2); A. c. lunulata (0/1); Anthornis melanura (1/1); Certhionyx niger (0/1); C. pectoralis (0/2); C. variegatus (0/1); Conopophila albogularis (0/1); C. rufogularis (0/1); C. whitei (0/1); Entomyzon cyanotis (0/3); Grantiella picta (0/1); Lichenostomus chrysops (1/3); L. cratitius (0/2); L. frenatus (0/2); L. flavescens (0/3); L. hindwoodi (1/2); L. keartlandi (0/2); L. leucotis (0/2); L. ornatus (0/2); L. penicillatus (0/10); L. plumulus (0/1); L. unicolor (0/1); L. virescens (0/1); Lichmera indistincta (0/2); Manorina flavigula (0/1); M. melanocephala (0/6); M. melanophrys (0/3); Melidectes torquatus (0/1); Melilestes megarhyncha (0/1); Meliphaga gracilis (0/1); M. lewinii (0/2); M. notata (0/2); Melipotes fumigatus (0/1); Melithreptus brevirostris (0/2); M. gularis laetior (0/1); M. lunatus (0/2); Myzomela erythrocephala (0/ 1); M. obscura (0/3); M. sanguinolenta (0/2); Notiomystis cincta (1/0); Oedistoma iliolophus (0/1); Philemon argenticeps (0/1); P. buceroides (0/3); P. citreogularis (0/3); P. corniculatus (0/4); P. diemenensis (0/1); Phylidonyris albifrons (0/1); P. melanops (0/1); P. nigra (0/1); P. novaehollandies (0/2); Plectorhyncha lanceolata (0/1); Prosthemadera novaeseelandiae (0/2); Ptiliprora guisei (0/1); Ramsayornis fasciatus (0/1); R. modestus (0/ 1); Trichodere cockerelli (0/1); Xanthomyza phrygia (0/7); Xanthotis flaviventer (0/1) Meliphagidae: Epthianurinae (0/4): Ashbyia lovensis (0/2); Epthianura albifrons (0/1); E.

tricolor (0/1);

Superfamily Corvoidea (104/322)

- Petroicidae (65/131): Amalocichla incerta (2/0); Drymodes brunneopygia (1/17); D. superciliaris (0/1); Eopsaltria australis (10/12); E. georgiana (0/5); E. griseogularis (1/3); E. pulverulenta (0/2); Heteromyias albispecularis (1/1); H. cinereifrons (0/1); Melanodryas cucullata (1/13); M. vittata (1/2); Microeca fascinans (1/8); M. flavigaster (0/4); M. flavovirescens (0/3); M. papuana (0/3); Monachella muelleriana (0/1); Pachycephalopsis polisoma (0/3); Peneothello cyanus (0/5); P. sigillatus (0/1); Petroica australis (0/5); P. goodenovii (4/17); P. macrocephala (0/2); P. multicolor (11/4); P. phoenicea (14/1); P. rodinogaster (2/1); P. rosea (9/1); Poecilodryas albonotata (0/3); P. placens (0/1); P. superciliosa (0/3); P. s. cerviniventris (0/2); Tregellasia leucops (3/3); T. capito (4/3)
 Orthonychidae (5/0): Orthonyx spaldingii (1/0); O. temminckii (4/0)
- Pomatostomidae (8/0): Pomatostomus halli (1/0); P. ruficeps (2/0); P. superciliosus (2/0); P. temporalis (3/0);
- **Eupetidae** (2/2): Cinclosoma punctatum (0/2); Psophodes cristatus (1/0); P. olivaceus (1/0) Neosittidae (5/0): Daphoenositta chrysoptera (5/0)
- Pachycephalidae (4/33): Colluricincla harmonica (1/5); C. megarhyncha (0/3); C. woodwardi (0/3); Falcunculus frontatus (0/2); Mohoua albicilla (1/0), M. novaeseelandiae (1/0), M. ochrocephala (1/0); Pachycephala inornata (0/1); P. lanioides (0/1); P. olivacea (0/3); P. pectoralis (0/7); P. rufiventris (0/4); P. simplex (0/2); Pitohui nigrescens (0/1); Rhagologus leucostigma (0/1)
- incertae cedis (0/3): Turnagra capensis (0/3)
- Dicruridae: Monarchinae (1/20): Arses telescophthalmus (0/1); Clytorhynchus pachycephaloides (0/1); Machaerirhynchus flaviventer (1/0); Monarcha leucotis (0/1); M. melanopsis (0/4); M. trivirgatus (0/4); Myiagra alecto (0/3); M. cyanoleuca (0/1); M. inquieta (0/2); M. i. nana (0/2); M. rubecula (0/1)
- **Dicruridae: Rhipidurinae (0/33):** *Rhipidura fuliginosa* (0/10); *Rhipidura leucophrys* (0/10); *R. rufifrons* (0/10); *R. r. dryas* (0/2); *R. rufiventris* (0/1)

Dicruridae: Grallininae (0/6): Grallina bruijni (0/1); G. cyanoleuca (0/5) Dicruridae: Dicrurinae (0/2): Dicrurus bracteatus (0/2) Graham R. Fulton & Walter E. Boles

- **Campephagidae** (4/7): Coracina lineata (1/0); C. novaehollandiae (3/0); C. papuensis (0/2); C. tenuirostris (0/1); Lalage leucomela (0/2); L. sueurii (0/2)
- Oriolidae (0/11): Oriolus sagittatus (0/3); O. flavocinctus (0/2); Sphecotheres viridis (0/6)

Artamidae: Artaminae (0/14): *Artamus cyanopterus* (0/3); *A. leucorhynchus* (0/2); *A. minor* (0/2); *A. personatus* (0/3); *A. superciliosus* (0/4)

Artamidae: Cracticinae (0/14): *Cracticus nigrogularis* (0/2); *C. torquatus* (0/2); *Gymnorhina tibicen* (0/2); *Strepera graculina* (0/8)

Artamidae: Peltopsinae (0/1): Peltops montanus (0/1)

Paradisaeidae (2/7): Cicinnurus regius (0/1); Epimachus meyeri (0/1); Lophorhina superba (0/1); Manucodia comrii (2/0); M. keraudrenii (0/1); Parotia lawesi (0/1); Ptiloris magnificus (0/1); P. victoriae (0/1)

Corvidae (0/9): Corvus bennetti (0/5); C. coronoides (0/2); C. mellori (0/1); C. orru (0/1) **Corcoracidae (2/6):** Corcorax melanorhamphos (2/0); Struthidea cinerea (0/6)

Ptilonorhynchidae (0/22): Ailuroedus crassirostris (0/3); A. melanotis (0/1); Amblyornis subalaris (0/1); Chlamydera cerviniventris (0/1); C. maculata (0/3); C. nuchalis (0/1); Prionodura newtoniana (0/1); Ptilonorhynchus violaceus (0/4); Scenopoeetes dentirostris (0/1); Sericulus chrysocephalus (0/6)

Callaeatidae (6/1): Callaeas cinerea (4/0); Philesturnus carunculatus (2/0); Heterolocha acutirostris (0/1)

Parvorder Passerida (113/10)

Superfamily Fringilloidea (55/6)

Alaudidae (0/3): Alauda arvensis (0/2); Mirafra javanica (0/1)

Motacillidae (2/1): Anthus novaeseelandiae (0/1); Motacilla alba (2/0)

Passeridae: Passerinae (4/0): Passer domesticus (4/0)

Passeridae: Estrildinae (28/1): Emblema pictum (1/0); Erythrura gouldiae (1/0); E. trichroa (2/0); Heteromunia pectoralis (1/0); Lonchura castaneothorax (0/1); L. oryzivora (1/0); Neochmia phaeton (1/0); N. ruficauda (3/0); N. temporalis (2/0); Poephila acuticauda (3/0); P. cincta (3/0); P. personata (2/0); Stagonopleura bella (2/0); S. guttata (2/0); Taeniopygia bichenovii (2/0); T. guttata (2/0)

Fringillidae (6/1): Carduelis carduelis (3/0); C. tristis (3/0); Fringilla coelebs (0/1)

Emberizinae (2/0): Emberiza calandra (1/0); E. citrinella (1/0)

Nectarinidae (1/0): Nectarinia jugularis (1/0)

Dicaeidae (4/0): *Dicaeum hirundinaceum (1/0); Melanocharis niger (1/0); Oreocharis arfaki* (1/0); *Rhamphomantis crassirostris (1/0)*

Superfamily Sylvioidea (33/2)

Hirundinidae (11/0): *Hirundo ariel* (4/0); *H. neoxena* (6/0); *H. nigricans* (1/0) Pycnonotidae (0/2): *Pycnonotus jocosus* (0/2)

Sylviidae (13/0): Acrocephalus stentoreus (1/0); Cincloramphus cruralis (2/0); C. mathewsi (3/0); Cisticola exilis (2/0); Eremiornis carteri (2/0); Megalurus gramineus (1/0); M. (Bowdleria) punctata (1/0); M. timoriensis (2/0)

Zosteropidae (9/0): Zosterops lateralis (6/0); Z. luteus (2/0); Z. strenuus (1/0) Superfamily Muscicapoidea (25/2)

Muscicapidae (13/0): *Turdus merula* (2/0); *T. philomelos* (2/0); *T. poliocephalus* (3/0); *Zoothera lunulata* (6/0);

Sturnidae (12/2): Acridotheres tristis (2/0); Aplonis cantaroides (1/0); A. fusca (4/0); A. metallica (0/2); Sturnus vulgaris (5/0)

of the Corvidae *sensu* Sibley & Ahlquist (1990) and Sibley & Monroe (1990). In this, it parallels the distribution of a single pneumotricipital fossa in these groups. This contrasts with the Passerida, in which the predominant states are the absence of a sternal pneumatic fossa and the presence of a double pneumotricipital fossa.

This segregation of character states between the Corvida and Passerida is marked, but not absolute, and there are some intriguing discrepancies, particularly in the former group. In the Menuroidea, the treecreepers are conspicuous by lacking the sternal fossa. The placement of these birds in this superfamily has been problematic, and Sibley & Ahlquist (1990), who proposed it, nonetheless expressed doubts about this action. Within the Meliphagoidea, there is a distinct division between the Pardalotidae (including the Acanthizinae) and Maluridae on one hand, and the Meliphagidae on the other. The presence of pneumatic foramina in the chats (*Epthianura, Ashbyia*) supports their association with the honeyeaters rather than the acanthizid warblers (Christidis *et al.* 1993).

There is no obvious pattern in the distribution of character states within the Corvoidea, other than the apparent correlation between this character and the pneumotricipital fossa, mentioned above. The placement of the *Mohoua* in the Pachycephalidae (Keast 1977, Sibley & Ahlquist 1987) has been challenged (Olson 1990a). The absence of sternal pneumatisation in the three species of *Mohoua* contrasts with the presence state in all but one of the other pachycephalid specimens examined. The taxonomic placement of *Turnagra* remains unresolved (e.g. Christidis *et al.* 1996). Because this genus shares the presence of pneumatic foramina with the families with which it has been associated (Ptilonorhynchidae/Paradisaeidae, e.g. Olson *et al.* 1983, Christidis *et al.* 1996, Pachycephalidae, e.g. Mayr 1967), this character adds no support for either alternative.

The Passerida exhibit a greater uniformity than the Corvoidea, with the character state 'absent' being found in all but a few of the sampled taxa. These species are unequivocally placed in the Passerida by molecular studies. The bulbuls also differ from the 'normal' condition of the Passerida by having a single pneumotricipital fossa (Olson 1990b). (It is notable that the waxwings, Bombycillidae, whose placement in the Passerida has never been questioned, also have a single pneumotricipital fossa (Bock 1962) and prominent pneumatic foramen of the sternum (pers. obs.)).

It is possible that, because most of the sample sizes are small, these may not accurately reflect the amount of variation within a species. In the robins (Petroicidae), for which sample sizes were considerably larger, the occurrence in a species of both character states was more widespread. This could be a property of this family, however, as they also have a range of intermediate states in the pneumotricipital fossa (pers. obs.).

The range of variation encompassed by the state 'present' is quite broad (Fig 1be), and it is likely that it will be possible to subdivide it into two or more states. Although the expression of this character may be related to age, no obvious relationship was discerned between the maturity of the bird (as indicated by degree of cranial pneumatisation) and the character state. In specimens of Eastern Yellow Robin *Eopsaltria australis*, the character states were about evenly distributed between birds with unpneumatised and fully pneumatised skulls.

This character invites further study. At present, it must be considered just one character that can be used in concert with others, but is by itself an insufficient basis on which to make taxonomic decisions. It may be usefully re-evaluated in light of more recent modifications of passerine phylogeny (e.g. Barker *et al.* 2002; Ericson *et al.* 2002).

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A newly discovered paralectotype of Pteroptochos megapodius Kittlitz, 1830

by F. D. Steinheimer

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In 1834, John Edward Gray (1800-1875) of the British Museum, now The Natural History Museum (BMNH), started an extended exchange with Eduard Rüppell (1794-1884) from Frankfurt am Main receiving at least 20 of Rüppell's Abyssinian types (Rüppell 1835-40, 1845) (Steinheimer, in press).

Among the BMNH Rüppell specimens is also a single bird from Chile, a Moustached Turca *Pteroptochos megapodius* (BMNH reg. no. 1842.8.16.27), which was the first of this species to reach the BMNH. No entry for this specimen was found in the old BMNH Vellum catalogues, where many of Rüppell's birds were listed, showing that the specimen had been received as part of a later exchange between 1837 and 1842 (Knox & Walters 1992).

As Rüppell never went to Chile, this early Chilean specimen in Rüppell's museum at Frankfurt probably came from Baron Friedrich Heinrich von Kittlitz (1799-1874), whose Chilean collection (March-April 1827) went partly to Frankfurt (Steinbacher 1954), but also to Berlin and St. Petersburg. This specimen is unlikely to have been part of the collection of another German, Eduard Friedrich Pöppig (1798-1868),